EARLY WARNING CUES FOR SOCIAL WASPS ATTACKED BY ARMY ANTS*

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Colonies of social insects are well protected from most intruders by stings, bites, defensive chemicals, and nest architecture (Wilson 1971, Jeanne 1975). Army ants of the Neotropical genus *Eciton,* however, prey heavily on a wide variety of ants (Formicidae) and social wasps (Vespidae:Polistinae) (Rettenmeyer 1963, Schneirla 1971). Natural and staged raids observed on Barro Colorado Island, Panama Canal Zone, revealed how army ants break through defensive barriers of insect colonies. Surprisingly, though social wasps are often aggressive and larger than army-ant workers, most showed little or no attempt to defend their colonies and usually abandoned their nests after only brief contacts with the invading ants. Such rapidity of departure suggests 1) that the wasps use some mechanism other than direct contact with the raiding ants to detect the threat, and 2) that the wasps may "recognize" army ants with some specificity. To investigate these two possibilities the social wasp species *Protopolybia exigua binominata* (Schulz) was observed during raids and tested for its ability to detect army ants.

Observations and Tests

Protopolybia exigua is a small (length = 5mm) social wasp that makes a flat oval or hexagonal nest 4 to 12 cm long (Fig. 1). The single horizontal comb is attached to the underside of a leaf by several short petioles and is enclosed by a carton envelope having a small entrance near the edge of the upper nest surface. There may be 30 to several hundred adult wasps in a colony. Nests are attached to a variety of plants, usually on leaves one to 4 m above the ground, at sites which are frequently explored by raiding army ants. Colonies of this wasp were observed to be raided by *Eciton burchelli* four times and by *E. hamatum* 10 times during two study periods totaling 19 weeks on Barro Colorado Island.

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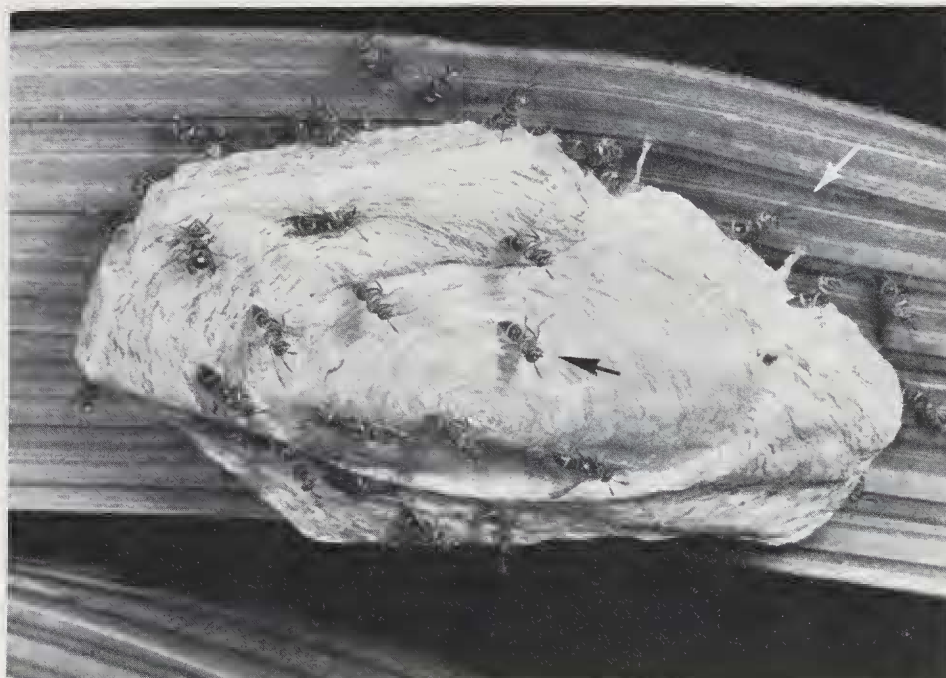

Fig. 1 Nest of *Protopolybia exigua* on the underside of a palm leaflet with wasps showing group alarm behavior. Arrows indicate two of many individuals giving alarm.

As soon as army ants approached within several centimeters of a *P. exigua* nest, wasps rushed to the lower nest surface and adjacent leaf. One to several wasps fanned their wings intermittently, and simultaneously produced a buzzing sound. Within seconds other wasps joined in the sound production, and the initial disorganized fanning and buzzing became regular, synchronous pulses. This complex synchronized behavior is termed "group fanning." The buzzing was most likely produced by the vibration of the thoracic skeleton by the indirect flight muscles. Fanning without sound production is a generalized behavior pattern, but fanning with buzzing was observed only in alarm situations.

Not all the wasps in the colony participated in the alarm: the number varied from several to 20 or more, depending in part on the strength of the alarm stimulus. Each buzz was about 0.9 sec long, followed by a 1.3 sec pause, and during its production the tip of the wasp's gaster was pressed to the substrate with head and front legs lifted (Figs. 1, 2). Between pules the body returned to the normal

Fig. 2 *Protopolybia exigua* participating in group alarm: front legs raised, wings fanning, and gaster pressed to substrate. A few wasps may begin the alarm; others join in.

resting position. Contact between the gaster and carton during the buzzing vibrated the envelope and nest leaf probably communicating alarm to other wasps (West-Eberhard 1969: 16, Naumann 1970: 120). Naumann (1970) described a similar behavior for *Protopolybia acutiscutis (=pumila)*, but it has not been reported for other polistine genera.

Group fanning continued until the first three or four army ants ran onto the nest. At that point the wasps flew from the nest in unison. In one raid observed, army ants ran back and forth for 10 minutes on the leaf supporting a wasp nest before making actual contact with the wasps; the wasps exhibited group fanning during the entire period.

Clearly, the wasps did not use physical contact to detect the army ants; the form, movement, or odor of the army ants probably alarmed the wasps. The efficacy of a visual cue in eliciting alarm from the wasps was tested by placing a single army ant in a clear, sealed vial and holding it in 30-cm forceps 1 cm from a *P. exigua* nest. Tests were conducted only when there was a minimum of three wasps on the nest surface. As a control the same vial (ant inside) was covered with opaque tape and was tested similarly. During the tests the army ants typically ran back and forth in the vial. A third test was therefore done to investigate the effect of movement of the ant: a dead ant was placed in a clear, sealed vial and tested.

The responses of the wasps were scored in 3 categories: alarm (group fanning), "alert", and no response (Table 1). The moving ant consistently elicited alarm, the dead ant alert, and the control vial no response. These results demonstrate that the movement of the army ant is an important component of the alarm cue. However, numerous other observations on *P. exigua* showed that the wasps' response to a moving army ant was not specific but a generalized alarm response to small moving objects. Phorid flies, spiders and various non-army-ant species elicited alarm when wasps saw them or their shadows through the leaf to which the nest was attached. Tips of forceps elicited alarm when moved rapidly back and forth above a nest leaf but not when held motionless.

To test whether odors of army ants might also elicit alarm from the wasps two procedures were used: 1) single army ants were crushed in forceps, concealed between the tips and held 1 cm from a nest for 2 min, or 2) 10 whole army ants were extracted in 1 ml of solvent (methylene chloride) and 10 μl of the extract applied to the

Table 1. Response of *Protopolybia exigua* to visual tests of army ants in vials.

Test	Group Fanning	Alert	No Response
moving ant	14	1	0
dead ant	1	5	5
moving ant concealed	0	1	12

end of a strip of paper 1 × 7 cm which was then held 1 cm from a nest for 2 minutes. Clean forceps and paper strips with 10 μl of solvent were similarly tested as controls. For comparison six other ant species were tested, either crushed or extracted, and 3 chemicals known to be components of ant pheromones were tested by applying 0.5 μl to a strip of paper and tested as for the ant extracts. Tests of clean forceps and untreated paper strips were controls for those tests. Tests were conducted at a total of 53 nests of *P. exigua*, and the number and order of tests varied at each nest (Table 2).

The wasps were tested for a response to 2 other army ants, *Nomamyrmex esenbecki* and *Neivamyrmex pilosus* in addition to *Eciton burchelli* and *E. hamatum*. Army ants of the former two genera have odors distinct from those of *Eciton* (Rettenmeyer 1963: 295), and though *Nomamyrmex* is known to raid wasps, such raids are probably rare (Chadab 1979). Non-army-ant species used in these tests were *Azteca* sp. and *Monacis bispinosa* (Dolichoderinae), *Camponotus sericeiventris* (Formicinae), *Ectatomma tuberculatum* and *Paraponera clavata* (Ponerinae), all of which are common terrestrial and aboreal scavengers and predators on other insects, but are not known to prey upon wasps.

Chemicals tested were 1) citral, an alarm substance which has been identified from the mandibular glands of 2 ant species in 2 subfamilies (Formicinae, Myrmicinae); 2) formic acid, which occurs in all members of the subfamily formicinae and is sprayed as an offensive-defensive chemical; and 3) 4-methyl-3-heptanone, which "appears to be the most widespread alarm pheromone. . .in the Formicidae" occurring in members of 4 ant subfamiies (Ecitoninae, Myrmicinae, Ponerinae, Pseudomyrmicinae) (Blum 1973 and references contained therein).

The wasps were commonly alerted by the test object, walking on the nest, raising their antennae, and orienting toward the object. Those activities demonstrated an awareness of the test object, but tests were considered positive only if at least 3 wasps participated in

Table 2. Group fanning of *Protopolybia exigua* to odors.

Tests	Trials	Group N	Fanning %
Crushed single ants			
Azteca sp.	15	1	7
Camponotus sericeiventris	23	6	26
Eciton burchelli	40	28	70
Eciton hamatum	14	10	71
Ectatomma tuberculatum	9	0	0
Paraponera clavata	13	0	0
forceps control	27	2	7
Ant extracts			
Eciton	18	12	67
Monacis bispinosa	6	0	0
Neivamyrmex pilosus	8	0	0
Nomamyrmex esenbecki	10	1	10
solvent, methylene chloride	27	0	0
Chemicals			
citral	14	0	0
formic acid	11	8	73
4-methyl-3-heptonone	6	0	0
paper control	44	0	0

group fanning. The data summarized in Table 2 show that of all the crushed and extracted ants, chemicals, and controls tested, only the 2 *Eciton* species, *Camponotus sericeiventris,* and formic acid elicited group alarm in significant numbers of tests ($P < .005$, as determined by chi-square analysis). The response of *C. sericeiventris*, was significantly lower than to the *Eciton* species and the synthetic formic acid ($P < .005$). Most likely, formic acid which occurs in *C. sericeiventris* causes the alarm response of the wasps to that ant species as well. The 0.5 μl of synthetic formic acid tested falls within the range of a single-ant amount (Stumper 1952), but the odor seemed subjectively stronger than the crushed *C. sericeiventris*. This may explain why the synthetic formic acid evoked group fanning more effectively than the crushed ant.

I conclude that *Eciton* odor is highly effective in eliciting alarm from *P. exigua.* Together, the 8 species of crushed ants and the 3 synthetic ant pheromones tested represent a selection of odors from all 6 Neotropical ant subfamilies (Brown 1973). If the alarm to *C. sericeiventris* is due to formic acid then only one substance other than *Eciton* odor actually evoked alarm. Although *P. exigua* does not respond exclusively to army-ant odor, the odor is a relatively specific alarm cue.

Another indication that the wasps discriminate army-ant odor with some specificity is the use by the wasps of primarily one alarm behavior in response to army ants. *P. exigua* possesses a repertoire of alarm responses: for example, disturbances which simulate a vertebrate predator such as my gently shaking the nest or my approach to the nest caused the wasps to retreat to the space between the upper surface of the envelope and the leaf; a sudden rap on the nest leaf caused the wasps to rush out onto the envelope flipping open their wings; while arthropods flying or walking next to the nest evoked buzzing and fanning by a single wasp and in some instances group fanning. Apparently, the wasps distinguish among types of disturbances and respond appropriately. This specific recognition of predator is similar to the "enemy specification" of the ant *Pheidole dentata* (Wilson, 1975).

Detection of army ants by sight and odor may be adaptive to the wasps for the following reasons. Once army ants discover a nest the wasps are unable to fend off the attack. The wasp brood cannot be rescued, but the adult population can flee and recolonize (Naumann 1975, Chadab 1979). Speed in evacuating the nest is crucial since the ants attack suddenly and in great numbers (Chadab and Rettenmeyer 1975). Using the sight or smell of army ants as a warning cue aids the wasps in preparation for a rapid evacuation: alarm is spread through the colony, the wasps run out of the tiny entrance in single file and spread out on the outside of the envelope. Flight occurs only after contact with the army ants, but the threshold for flight is reached with only one to several army ants. The wasps are able to fly instantly in almost a single wave. In most raids, nonetheless, several adults are seized by the ants because they are trapped inside the nest, become embattled with the first invading ants, or are sluggish teneral adults. Without an advance warning many more wasps would probably be trapped inside, and the threshold for flight might depend on considerably more direct contact with the ants. The result would be higher mortality of adult wasps.

The adaptive ability of *P. exigua* to detect *Eciton* odor probably resulted from selective pressure exerted by army ants. Since army ants prey upon numerous species and prey colonies are usually cropped rather than destroyed, the effect of army ants on any one species might be considered weak or negligible. However, response of *P. exigua* to army ant predation is evidence that army ants have had a tangible effect on at least that prey species.

I have observed other wasp species leave their nest promptly when besieged by army ants and have found that 16 of 31 other polistines also become alarmed by *Eciton* odors (Chadab 1979). Forsyth (1978) also reported that 3 species of Polistinae responded to army ant odors. Numerous ant prey have also been observed to flee (with their brood in contrast to social waps) in advance of an army-ant attack (pers. observ., Topoff 1975). Such evidence suggests that the early detection of army ants is common among ant and social-wasp prey and may be an important phenomenon in the invasion of social-insect colonies by army ants.

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Literature Cited

Blum, M. S.
1973. Comparative exocrinology of the Formicidae. Proc. VII Congr. IUSSI, London, p. 23–40.

Brown, W. L.
1973. A comparison of the Hylean and Congo-West African rain forest ant faunas. p. 161–185 in Tropical forest ecosystem in Africa and South America: A comparative review, Betty J. Meggers, et al. eds., Smithsonian Institution Press, Wash. D.C.

Chadab, R.
1979. Army-ant predation on social wasps. Unpublished Ph.D. Thesis, University of Connecticut. 260 p.

Chadab, R. and C. W. Rettenmeyer
1975. Mass recruitment by army ants. Science **188**:1124–1125.

Forsyth, A. B.
1978. Studies on the behavioral ecology of polygynous social wasps. Unpublished Ph.D. Thesis, Harvard University. 226 p.

Jeanne, R. L.
1975. The adaptiveness of social wasp nest architecture. Quart. Rev. Biol. **20**:267–287.

Naumann, M. G.
1970. The nesting behavior of *Protopolybia pumila* in Panama (Hym. Vespidae). Unpublished Ph.D. Thesis, University of Kansas. 182 p.
1975. Swarming behavior: Evidence for communication in social wasps. Science **189**:642–644.

Retenmeyer, C. W.
1963. Behavioral studies of army ants. Univ. of Kansas Sci. Bull. **44**:281–465.

Schneirla, T. C.
1971. Army ants: A study in social organization. H. R. Topoff, ed., Freeman, Calif. 349 p.

Stumper, M. R.
1952. Données quantitaives sur la secrétion d'acide formique par les fourmis. C. R. Acad. Sci., Paris **234**:149–152.

Topoff, H.
1975. Ants on the march. Nat. Hist. **84**:60–69.

West-Eberhard, M. J.
1969. The social biology of polistine wasps. Univ. Mich. Mus. Zool. Misc. Publ. **140**:1–101.

Wilson, E. O.
1971. The insect societies. Belknap Harvard Univ. Press, Cambridge, Mass. 548 p.
1975. Enemy specification in the alarm-recruitment system of an ant. Science **190**:798–800.